Coleochaete and the origin of sporophytes

Coleochaete and the origin of sporophytes[1]

David Haig[2,3]

2. Department of Organismic and Evolutionary Biology,

Harvard University, 26 Oxford Street,

Cambridge MA 02138 USA.

1 1. Manuscript received _____; revision accepted _____.

2 3. Author for correspondence (e-mail: dhaig@fas.harvard.edu)

Premise of study: Zygotes of *Coleochaete* are provisioned by the maternal thallus before undergoing 3–5 rounds of division to produce 8–32 zoospores. An understanding of the selective forces favoring post-zygotic divisions would be relevant not only to the life history of *Coleochaete* but to the origin of a multicellular diploid phase in embryophytes.

Methods: Simple optimization models are developed of the number of zygotes per maternal thallus and number of zoospores per zygotes.

Key results: Zygotic mitosis is favored once zygotes exceed a threshold size but natural selection usually promotes investment in additional zygotes before zygotes reach this size. Factors that favor production of fewer, larger zygotes include multiple paternity, low fecundity and non-provisioning (accessory) costs of zygote production. Such factors can result in zygotes exceeding the size at which zygotic mitosis becomes profitable.

Conclusions: *Coleochaete* may possess large zygotes that undergo multiple fission because of accessory costs associated with matrotrophy (cellular cortex, unfertilized oogonia). The unpredictability of fertilization on land is proposed to have increased accessory costs from unfertilized ova and, as a consequence, to have favored the production of larger zygotes that underwent postzygotic division to produce diploid sporophytes.

Key words: *Coleochaete*, sporophyte, alternation of generations, size-versus-number, matrotrophy

Many nineteenth-century botanists considered the multicellular 'fruits' (zygospores) of *Coleochaete* to be analogous, perhaps even homologous, to the sporophytes of land plants. Supporters of both the homologous and antithetic theories of the origin of sporophytes used the 'fruit' as a model but disagreed about how it should be interpreted, whether as a modified asexual generation or as a novel interpolated structure (Haig 2008). *Coleochaete* fell from favor in these debates after Allen (1905, 1906) concluded that the first two divisions of its zygospore were the heterotypic and homotypic divisions (in modern parlance, meiosis I and II). Since then, the 'fruit' has generally been interpreted as a haploid rather than diploid structure.

Interest in *Coleochaete* has revived with recognition that it belongs among the closest algal relatives of embryophytes (Ruhfel et al. 2014). The absence of a multicellular diploid phase in streptophyte algae is now considered strong support for the antithetic theory because it weakens the case for an ancestral isomorphic alternation of generations as envisioned in modern versions of the homologous theory (Blackwell 2003; McManus and Qiu 2008). Clearly, contemporary arguments about homologous versus antithetic alternation of generations bear only a tenuous relation to the morphological questions at the heart of the nineteenth-century debate (Haig 2008). Although the 'fruit' has lost favor as an analogue of sporophytes, matrotrophy has gained prominence as a feature shared by *Coleochaete* and embryophytes. *Coleochaete* zygotes increase in size and accumulate reserves after syngamy, suggesting that the haploid maternal parent transfers resources to the diploid product of fertilization (Graham and Wilcox 1983, 2010).

Although the occurrence of zygotic meiosis in *Coleochaete* is generally accepted, evidence in support of this 'common knowledge' is thin. Allen (1905) was unable to count chromosomes but concluded that the first two divisions of zygospores were meiotic on the basis of differences in chromosome compaction. On the other hand, Hopkins and McBride (1976) detected nuclei with eight times the unreplicated haploid quantity of DNA (8C) within germinating zygospores. A division sequence that reduces DNA levels from 8C to 1C corresponds to neither meiosis nor mitosis as conventionally understood (Haig 2010).

This paper presents simple life-history models of the transition from a single-celled zygote to a multicelled 'fruit.' These models are agnostic about the precise nature of *Coleochaete*'s postzygotic divisions whether meiotic, mitotic, or something else. Zygotes are assumed to develop attached to a multicellular maternal thallus. Therefore, developmental mechanisms required for postzygotic multicellularity are assumed already to be present and expressed in prezygotic parents (for a discussion of the origin of these mechanisms see Niklas 2014). Although my focus is on understanding life-history evolution and variation in *Coleochaete*, implications for early stages in the origin of sporophytes in embryophytes will also be considered.

SIZE-VERSUS-NUMBER TRADEOFFS

Haploid parents will be called mums and dads to distinguish them from diploid mothers and fathers (Haig 2013). Two size-versus-number tradeoffs will be considered. The first is faced by mums: whether to produce a few large or many small zygotes. The

second is faced by zygotic offspring: how many zoospores to produce from a zygote's reserves. These interrelated questions can be conceptualized as asking how should a mum allocate an amount Z among n zygotes each of which produces m zoospores.

Coleochaete filaments produce oogonia one at a time whereas the postzygotic divisions involve successive bipartitions of the zygospore cytoplasm without an increase in zygospore size (multiple fission or palintomy). Therefore, the number of zygotes will be assumed to change by integral increments (n, $n + 1$, $n + 2$, …) but the number of zoospores per zygote by successive doublings (m, $2m$, $4m$, …). My models address the specific question under what conditions natural selection favors a change from producing m to $2m$ zoospores per zygote. The fitness contribution of each zoospore will be represented by a function, $f(x)$, where x is a measure of the zoospore's nutrient reserves. Following Smith and Fretwell (1974), $f(x)$ is assumed to increase with x subject to diminishing marginal returns, i.e. $f''(x) < 0 < f'(x)$, with some minimum positive value of x below which $f(x) = 0$. Maternal fitness is $mnf(x)$. Thus zoospores are assumed to make independent contributions to maternal fitness determined by zoospore 'size' x.

Let maternal investment consist solely of zoospore reserves. A mum who invests a total amount Z in zygote production invests $X = xm$ in each of $n = Z/X$ zygotes. Z is optimally distributed when each zygote receives $\hat{X} = m\hat{x}$ where $\hat{x}$ is the investment per zoospore at which marginal returns on investment equal average returns

$$f'(\hat{x}) = \frac{f(\hat{x})}{\hat{x}}$$

Mums are predicted to respond to variation in Z by varying the number rather than the

size of zygotes (Smith and Fretwell 1974; Lloyd 1987).

Under the assumption that $f''(x) < 0 < f'(x)$, there will be a critical investment x^* for which $f(x^*) = 2f(x^*/2)$. For a zygote of size X, higher fitness would be obtained by dividing X among m zoospores for $X < mx^*$, but by dividing X among $2m$ zoospores for $X > mx^*$. However, the optimal size of zoospores is less than this critical size, $\hat{x} < x^*$ (Fig. 1). If mums always produced zygotes of size $\hat{X} = m\hat{x}$, then these zygotes would be smaller than the 'size' at which an extra division becomes profitable.

Changes in Z and X are continuous but changes in m and n occur by integral steps. At least one zoospore must receive more or less than $\hat{x}$ if Z is not a precise multiple of $\hat{X}$. Suppose that $n\hat{X} < Z < (n+1)\hat{X}$ where $Z = n\hat{X} + \Delta Z$. For ΔZ close to zero, Z is better distributed evenly among n zygotes but, for ΔZ above some critical value, Z is better distributed evenly among $n + 1$ zygotes. As ΔZ approaches this critical value, optimal zoospore size approaches x' then abruptly decreases to x'' as the mum switches from investing in n to $n + 1$ zygotes where $nf(x') = (n + 1)f(x'')$. As n becomes large, x' and x'' converge on $\hat{x}$. Conversely, low fecundity (small n) favors greater variation in zygote size as Z fluctuates. The difference between x' and x'' is maximal for $n = 1$ when $x' = x^*$ and $x'' = x^*/2$. In the special case when $Z = X^* = mx^*$, three alternatives yield the maximum return on investment (i) a single zygote that produces m zoospores of size x^*; (ii) two zygotes that each produce m zoospores of size $x^*/2$; or (iii) a single zygote that undergoes an extra division to produce $2m$ zoospores of size $x^*/2$.

The above model predicts that adaptive adjustment of x will be achieved by changing n (number of zygotes) rather than m (number of zoospores per zygote) except

when n is small. The addition of an extra postzygotic division involves an abrupt halving of zoospore size from x to $x/2$ whereas addition of an extra zygote involves a smaller decrease in zoospore size in the ratio $n + 1$ to n. Thus, for $n > 1$, zoospore number can be adjusted more smoothly by varying n rather than m. Control of m can be likened to adjusting the coarse focus on a microscope and control of n to adjusting the fine focus. Under the assumption that zoospore size is already close to optimal, improvements are more likely to be made with the fine focus than the coarse focus (Fisher 1958, p. 44).

ACCESSORY COSTS

An accessory cost is a cost of offspring production that is paid independently of the provisioning cost. Accessory costs shift the optimal size-versus-number trade-off in the direction of fewer, larger offspring (Haig and Westoby 1991). This is because increments in the provisioning cost per offspring are associated with smaller decrements in offspring number as the accessory cost per offspring increases. For example, materials invested in zygote walls and corticating cells would be considered accessory costs, as would costs of producing ova that remain unfertilized, or zygotes that abort before being provisioned (Haig 1990). In the context of the models of this paper, accessory costs may affect the probability of zygospore survival before zoospores are released but a zoospore's fitness once it is released is determined solely by the provisioning cost x.

Suppose that maternal fitness is proportional to $mnf(x)$ but that the cost of a zygote includes an accessory cost A such that the cost per zygote is $A + X$ and the cost per zoospore is $a + x$ where $m = A/a = X/x$. Thus, the model of the previous section

corresponds to the special case where $A = 0$ and maternal investment consists solely of partible provisions X. In the more general model of this section, a mum invests $A + X$ in each of $n = Z/(A + X)$ zygotes and the optimal zoospore size is

$$f'(\hat{x}) = \frac{f(\hat{x})}{a + \hat{x}}$$

An additional postzygotic division increases maternal fitness when $a > a^*$ where a^* is the accessory cost per zoospore at which $\hat{x} = x^*$ (Figure 2). At a^*, a zygote that produced $2m$ zoospores each of cost $(a^* + x^*)/2$ would yield the same return on investment as a zygote that produced m zoospores of cost $a^* + x^*$. However, if some zygotes produced m zoospores and others $2m$ zoospores at $a = a^*$, then mums would increase their fitness by reallocating investment from m-zygotes to $2m$-zygotes because the latter provide a higher marginal rate of return, $f'(x^*/2) > f'(x^*)$. As a consequence, the optimal size of $2m$-zygotes is greater than the optimal size of m-zygotes. By contrast, the optimal size of zoospores from $2m$-zygotes ($\tilde{x}$) is smaller than the optimal size of zoospores from m-zygotes because

$$f'(\tilde{x}) = \frac{f(\tilde{x})}{a/2 + \tilde{x}}$$

(Figure 2). Thus, a shift from m to $2m$ zoospores per zygote is predicted to be associated with fewer, larger zygotes but with more numerous smaller zoospores.

This model can be applied to each successive doubling of zoospores per zygote ($m = 4, 8, 16, \ldots$). For given Z, n (maternal fecundity) decreases as m (zygote fecundity) increases. An implication is that x (provisions per zoospore) becomes more variable for variable small Z. For given $f(x)$, each additional division requires twice the accessory cost

and provisioning cost per zygote to favor the next division. Because the critical accessory cost per zygote that is necessary to favor another division doubles for each extra division, selection to minimize accessory costs may place an upper bound on the number of divisions and zoospore number per zygote.

WHAT ABOUT SEX?

All zygotes inherit a mum's entire haploid genome (maternal relatedness $r_m = 1$). Therefore, optimal allocations are identical for mums and for maternal genomes of zygotes. Previous sections view the allocation of resources from this haploid maternal perspective, but intergenerational and intragenomic conflict can arise because zygotes also have dads (Haig and Wilczek 2006).

Paternal relatedness of a mum's zygotes, r_p, measures shared haploid paternity. Maternal and paternal genomes favor the same allocation of resources when all zygotes have the same dad ($r_m = r_p = 1$), but paternal genomes favor greater allocation to their own zygotes when zygotes have multiple dads ($r_p < 1$). Maternal investment in zygotes fathered by other dads can be conceptualized as an increased accessory cost per zygote from the perspective of each zygote's paternally-derived genes (Haig 1992). The less the value of r_p the greater the optimal size of a zygote from this paternal perspective.

If imprinted or unimprinted paternal genes influence the acquisition of reserves by zygotes, then paternal genes will favor greater acquisition than maternal genes. In the limit, when $r_p = 0$, paternal genes favor commitment of all maternal investment to their zygote. Thus maternal and paternal genes of zygotes are predicted to favor different

levels of resource acquisition from mum. Despite this conflict over zygote size, maternal and paternal genomes would agree on an extra division of the zygote whenever $x > x^*$.

Sexual reproduction generates novel genotypes. Svedelius (1927) proposed that postzygotic divisions confer an evolutionary advantage because a delay of meiosis "secures to the plant the possibility of bringing about numerous reduction divisions and thereby numerous character combinations." This argument is dubious. Consider a comparison between (i) a mum that produces n zygotes that produce $4n$ zoospores by meiosis versus (ii) a mum that produces a single zygote that divides to produce n sporocytes that divide by meiosis to produce $4n$ zoospores. If a single dad produced the sperm that fertilized every zygote then the two scenarios are genetically equivalent because all zygotes in either scenario have the same dad and mum ($r_m = r_p = 1$), and possess identical diploid genotypes. However, if $r_p < 1$ then (i) results in multiple diploid genotypes and greater genetic variation among zoospores than (ii). Although an extra division doubles the number of recombinant haploid genotypes generated from a single zygote, it reduces the diversity of offspring of a haploid parent if the alternative is production of an extra zygote.

Greater diversity of a mum's offspring is achieved by producing zygotes with multiple dads rather than a single dad. But from each dad's perspective, increased diversity of a mum's haploid partners reduces the number, but does not increase the genetic variability, of his offspring. If every zygote had a different dad, $r_p = 1$, then each dad would clearly favor maximizing maternal investment in his zygote at the expense of his rivals' zygotes. The major advantage of scenario (ii) relative to scenario (i) from a

paternal perspective is that maternal investment is not 'wasted' on offspring of other dads.

UNDERSTANDING *COLEOCHAETE*

A key question about the life cycle of *Coleochaete* has now been identified. Why should maternal thalli produce 32 zoospores from a single large zygospore when greater genetic diversity of offspring could be achieved by producing 32 zoospores from eight smaller zygotes? The models identified three factors that favor larger zygotes. First, larger accessory costs favor greater maternal investment per zygote. Second, postzygotic gene expression may enable paternal genes of zygotic offspring to take more than the maternal optimum. Third, low fecundity causes zygote size to fluctuate with available resources so that zygotes occasionally approach the size that favors an extra division.

The origin of matrotrophy was probably associated with increased accessory costs of zygospore production. Neighboring maternal filaments envelop *Coleochaete* zygotes after fertilization to form a cortex that probably has protective and nutritive functions. Cortical cells of some species develop elaborate wall in-growths that are believed to deliver nutrients to the expanding zygote (Graham and Wilcox 1983, 2000). The cortex may comprise a substantial part of the cost per zygote. Zygospores of *Coleochaete areolata*, for example, reach diameters of 75 μm enclosed in 'spermocarps' of 125 μm diameter (Entwisle and Skinner 2001).

Provisioning of zygotes after fertilization, rather than provisioning of oogonia before fertilization, means that maternal resources can be reallocated from unfertilized

to fertilized oogonia and creates opportunities for mums to abort low-quality zygotes. From a maternal perspective, costs of unfertilized oogonia and unprovisioned zygotes are accessory costs of the production of provisioned zygotes (Haig 1990). The evolution of matrotrophy also meant that the paternal genomes of zygotes could influence maternal investment in favor of larger zygotes (Haig and Wilczek 2006). Finally, the diminutive thalli, with relatively large zygospores, of *Coleochaete* are less fecund than thalli of larger multicellular algae and should therefore be subject to greater fluctuation in optimal zygospore size.

Cell growth without division followed by rapid division without growth is a feature of the life cycle of many green algae, known as multiple fission or palintomy (Bisová and Zachleder 2014). Temporal separation of growth and cell division may allow favorable conditions for growth to be fully exploited without pauses for division (Cavalier-Smith 1980). *Chlamydomonas* cells, for example, grow during the day but undergo multiple fission at night (Craigie and Cavalier-Smith 1982). *Coleochaete* zygotes similarly grow to full size before entering dormancy then undergo multiple divisions without growth after exit from dormancy. Zygotic palintomy may have evolved in *Coleochaete* because time-out for cell divisions would reduce competitiveness in the scramble for maternal investment among the zygotic progeny of a single mum.

Zygotic palintomy constrains the number of zoospores per zygote to increase by successive powers of two ($m = 4, 8, 16, \ldots$) and means that the first zygotic division is most difficult because the volume of cytoplasm to be divided is greatest. The models of this paper were crafted to conform to the observed development of *Coleochaete*. One can

envisage two relaxations of the constraints imposed by zygotic palintomy, both of which have been relaxed in the development of sporophytes. The first would be to allow cell division to occur during (rather than after) zygotic growth and provisioning. This would mean that earlier divisions in the sequence would occur in cells of smaller size. The models of this paper make no assumption about the timing of cell division and would therefore be unaffected by relaxation of this constraint. The second would be to relax the constraint that all cells divide at the same time and allow m to change less coarsely than by powers of two. This would fundamentally change the models.

VARIATION WITHIN *COLEOCHAETE*

Molecular divergence between *Coleochaete scutata* and *C. irregularis* is similar to that between *Oryza sativa* and *Ginkgo biloba* (Delwiche et al. 2002). *Coleochaete* thus contains comparable phylogenetic depth to the clade that includes all living seed plants and probably encompasses rich variation in reproductive biology and evolutionary ecology. Life-history variation within *Coleochaete* has been little studied. Therefore, this section will pose questions that may help frame future studies.

Coleochaete zygotes function as perennating structures. They remain uninucleate, and dormant, through winter until spring and then undergo multiple fission before all resulting cells are released as motile zoospores (Pringsheim 1860). The release of eight, 16 or 32 zoospores (Lee 1989) suggests a progression of three, four, or five rounds of division, but the process is probably not that regular. Oltmanns (1898) reported a variable number of divisions in *C. pulvinata* depending on zygospore size, with some

zygospores containing 24 cells because four cells had divided at the eight-cell stage and four had remained undivided.

Given the great age of the genus, one can ask why *Coleochaete* zygospores never produce four zoospores (two postzygotic divisions) or 64 zoospores (six postzygotic divisions). A possible explanation is that the limited variation in zoospore numbers is a consequence of developmental constraints. With respect to the minimum of eight zoospores, 8C nuclei have been observed in zygospores of *C. scutata* (Hopkins and McBride 1976) and the single zygotic chloroplast of *C. pulvinata* divides three times to produce eight chloroplasts before the zygote accumulates food reserves and enters dormancy (Oltmanns 1898). The nucleus of *C. pulvinata* does not divide until after winter dormancy at which time three nuclear divisions associate each chloroplast with a nucleus (Oltmanns 1898). If 8C zygotic nuclei are a conserved feature of *Coleochaete* then zygospores would need to undergo a minimum of three divisions to produce 1C zoospores.

One might speculate that the maximum of 32 zoospores per zygospore is similarly set by developmental constraints, in this case arising from difficulties of dividing larger reserve-filled zygospores. Although palintomic green algae typically produce 8–32 daughter cells per mother cell, the number of daughter cells per mother cell can be considerably larger in some taxa (Bisová and Zachleder 2014). Thus, there is no absolute constraint on higher orders of palintomy. Moreover, if mechanical difficulties preclude the production of 64 zoospores by successive bipartitions of a large zygospore, one might ask why zygotes do not divide first and then accumulate reserves

as occurs in bryophytes. Palintomic development has evolved into non-palintomic development (cell growth between divisions) multiple times in the multicellular green alga *Volvox* (Herron et al. 2010).

The maximum of five postygotic divisions in *Coleochaete* may be determined by a selective rather than developmental constraint. In this scneraion, additional divisions of larger zygospores would be developmentally possible but, beyond a certain zygospore size, higher maternal fitness is obtained by producing extra zygospores rather than larger zygospores. In the model of a previous section, each additional round of cell division required a doubling of the accessory (non-provisioning) cost per zygote. Other things being equal, natural selection will tend to favor smaller accessory costs because the more resources that are invested in accessory costs the less remain for provisioning zoospores. Selective constraints on the size of accessory costs may shift the size-versus-number trade-off toward smaller, more numerous zygotes.

Coleochaete zygotes are surrounded by a cortex of gametophytic cells. Cortication varies among species from complete enclosure of zygotes to sparse overgrowth by a few nearby filaments (Delwiche et al. 2002). More complete enclosure implies larger accessory costs and is therefore predicted to be associated with larger zygotes and more postzygotic divisions but, to my knowledge, the question whether zoospore numbers differ between fully-corticated and sparsely-corticated species has not been investigated.

Costs of unfertilized ova and aborted zygotes, and of waiting for fertilization, are accessory costs of zygospore production. *Coleochaete scutata* is dioicous (Pringsheim 1860) and produces many oogonia that abort without producing mature zygospores

(Wesley 1930). Fertilization is likely to be less reliable, and accessory costs of failed reproduction greater, in dioicous species than in monoicous species. Therefore, dioicous species might be expected to produce fewer, larger zygospores than otherwise comparable monoicous species. *C. scutata* produces dormant vegetative cells known as akinetes (Davis 1965). Therefore, these asexual propagules may perform some of the perennating functions of sexual zygospores. Akinetes could be considered insurance against sexual failure, with dioicous species predicted to invest more in akinetes than monoicous species.

ORIGIN OF SPOROPHYTES

Previous sections address the evolution of postzyotic divisions in *Coleochaete*. This final section considers selective factors in the origin of the multicellular sporophytes of land plants with a focus on the initial transition from zygotic meiosis to a few-celled sporophyte. The embryophyte life cycle will be assumed to have evolved from an ancestor with zygotic meiosis and to have initially possessed dependent sporophytes provisioned by maternal gametophytes as occurs in extant bryophytes.

The sporophytes of all living bryophytes differ from the multicellular 'fruits' of *Coleochaete* in several important respects. Zygospores of *Coleochaete* contain up to 32 cells, every one of which becomes a zoospore, whereas even the simplest sporophyte contains many thousands of cells including 'sterile' cells that do not undergo meiosis and do not differentiate as spores. If sporophytes had palintomic development like *Coleochaete* zygospores, then an enormous zygote would accumulate maximum reserves before its

cytoplasm underwent n rounds of division to produce 2^n cells (in a manner akin to the division of the giant cell of *Acetabularia*: Koop 1979). By contrast, embryophyte mums provision actively-dividing sporophytes with cell numbers that are not constrained to change by multiples of two. Other differences include the replacement of flagellated zoospores by wind-dispersed meiospores and transfer of the perennating phase with sporopollenin-containing cell walls from zygotes to meiospores (Brown and Lemmon 2011).

Svedelius (1927; also see McManus and Qiu 2008; Qiu et al. 2012) proposed that multicellular sporophytes conferred a great evolutionary advantage on land plants because postzygotic mitosis allowed many gene combinations to be generated from a single fertilization. However, Svedelius' hypothesis confounded genetic variability with number of spores because he did not consider the alternative of producing multiple zygotes (Wettstein 1943). More spores are better than fewer spores, even if the spores are genetically identical, but a mum could provision many zygotes for the cost of one large sporophyte. Greater genetic diversity of spores is achieved by provisioning n zygotes that produce $4n$ spores by zygotic meiosis than provisioning a single sporophyte that produces $4n$ spores because multiple zygotes can sample the allelic variation of multiple dads. Reduced genetic diversity of offspring is a cost of producing a sporophyte (*contra* Svedelius).

A venerable hypothesis posits that multicellular sporophytes evolved as a response to the rarity of fertilization on land allowing many spores to be produced from a single zygote (e.g., Bower 1890, p. 362; Campbell 1905, p. 567; Searles 1980). The rarity

of suitable conditions for fertilization can be overstated however. Bisexual gametophytes of monoicous mosses produce abundant sporophytes (Gemmell 1950) as do female gametophytes of many dioicous mosses when male gametophytes occur within the range of sperm movement (Longton and Greene 1969). Even if environmental conditions are rarely suitable for fertilization, the production of multiple zygotes would remain an effective alternative for producing many spores if suitable conditions were predictable in advance.

The models presented in this paper suggest that it was the unpredictability, not the rarity, of fertilization that favored zygotic amplification in land plants. If suitable conditions for fertilization are unpredictable and brief, then mums must produce archegonia without guarantee they will be fertilized. Suppose that such conditions occur erratically once every few months and that archegonia have limited longevity. A mum who produced several archegonia per month would 'waste' more resources on unfertilized archegonia than a mum who produced one archegonium per month. Although the number of unfertilized archegonia per zygote is the same for both kinds of mum, the cost of unfertilized archegonia per spore is lower for the mum who produces fewer archegonia but amplifies zygotic products. Higher accessory costs from unfertilized archegonia favor a shift in maternal investment toward fewer, larger zygotes. If these costs were sufficiently great, then optimal zygote size may have exceeded the size at which extra postzygotic divisions became profitable.

Allen, C. E. 1905. Die Keimung der Zygote bei *Coleochaete*. *Berichte der deutschen botanischen Gesellschaft* 23: 285-292.

Allen, C. E. 1906. The structure and division of the oospore in *Coleochaete*. *Science* 23: 133.

Bisová, K., and V. Zachleder. 2014. Cell-cycle regulation in green algae dividing by multiple fission. *Journal of Experimental Botany* 65: 2585–2602.

Blackwell, W. H. 2003. Two theories of origin of the land-plant sporophyte: which is left standing? *Botanical Review* 69: 125-148.

Bower, F. O. 1890. On antithetic as distinct from homologous alternation of generations in plants. *Annals of Botany* 4: 347–370.

Bower, F. O. 1908. *The origin of a land flora*. Macmillan, London.

Brown, R. C., and B. E. Lemmon. 2011. Spores before sporophytes: hypothesizing the origin of sporogenesis at the algal–plant transition. *New Phytologist* 190: 875–881.

Campbell, D. H. 1905. *The structure and development of mosses and ferns (Archegoniatae)*, second edition. MacMillan, New York.

Cavalier-Smith, T. 1980. *r*- and *K*-tactics in the evolution of protist developmental systems: cell and genome size, phenotype diversifying selection, and cell cycle patterns. *BioSystems* 12: 43–59.

Craigie, R. A. and T. Cavalier-Smith. 1982. Cell volume and the control of the *Chlamydomonas* cell cycle. *Journal of Cell Science* 54: 173–191.

Davis, J. S. (1965) The germination of the akinetes of *Coleochaete*. *Transactions of the American Microsopical Society* 84: 548–550.

Delwiche, C. F., K. G. Karol, M. T. Cimino, and K. J. Sytsma. 2002. Phylogeny of the

genus *Coleochaete* (Coleochaetales, Charophyta) and related taxa inferred by analysis of the chloroplast gene *rbcL*. *Journal of Phycology* 38: 394-403.

Entwisle, T. J., and S. Skinner. 2001. Non-marine algae of Australia: 4. Floristic survey of some colonial greem macroalgae (Chlorophyta). *Telopea* 9: 725–735.

Fisher, R. A. 1958. *The genetical theory of natural selection*. Second edition. Dover, New York.

Gemmell, A. R. 1950. Studies in the Bryophyta. I. The influence of sexual mechanism on varietal production and distribution of British Musci. *New Phytologist* 49: 64–71.

Graham, L. E., and L. W. Wilcox. 1983. The occurrence and phylogenetic significance of putative placental transfer cells in the green alga *Coleochaete*. *American Journal of Botany* 70: 113–120.

Graham, L. K. E., and L. W. Wilcox. 2000. The origin of alternation of generations in land plants: a focus on matrotrophy and hexose transport. *Philosophical Transactions of the Royal Society of London B* 355: 757–766.

Haig, D. 1990. Brood reduction and optimal parental investment when offspring differ in quality. *American Naturalist* 136: 550–556.

Haig, D. 1992. Genomic imprinting and the theory of parent-offspring conflict. *Seminars in Developmental Biology* 3: 153-160.

Haig, D. 2008. Homologous versus antithetic alternation of generations and the origin of sporophytes. *Botanical Review* 74: 395-418.

Haig, D. 2010. What do we know about charophyte (Streptophyta) life cycles? *Journal of Phycology* 46: 860–867.

Haig, D. 2013. Filial mistletoes: the functional morphology of moss sporophytes. *Annals of Botany* 111: 337–345.

Haig, D., and M. Westoby. 1991. Seed size, pollination costs and angiosperm success. *Evolutionary Ecology* 5: 231–247

Haig, D., and A. Wilczek. 2006. Sexual conflict and the alternation of haploid and diploid generations. *Philosophical Transactions of the Royal Society of London B* 361: 335-343.

Herron, M. D., A. G. Desnitskiy, and R. E. Michod. 2010. Evolution of developmental programs in *Volvox* (Chlorophyta). *Journal of Phycology* 46: 316–324.

Hopkins, A. W., and G. E. McBride. 1976. The life-history of *Coleochaete scutata* (Chlorophyceae) studied by a Feulgen microspectrophotometric analysis of the DNA cycle. *Journal of Phycology* 12: 29-35.

Koop, H.-U. 1979. The life cycle of *Acetabularia* (Dasycladales, Chlorophyceae): a compilation of evidence for meiosis in the primary nucleus. *Protoplasma* 100: 353–366.

Lee, R. E. 1989. *Phycology*. Second edition. Cambridge University Press, Cambridge, UK.

Lloyd, D. G. 1987. Selection of offspring size at independence and other size-versus-number strategies. *American Naturalist* 129: 800–817.

Longton, R. E., and S. W. Greene. 1969. Relationship between sex distribution and sporophyte production in *Pleurozium schreberi* (Brid.) Mitt. *Annals of Botany* 33: 107-126.

McManus, H. A., and Y.-L. Qiu. 2008. Life cycles in major lineages of photosynthetic eukaryotes, with a special reference to the origin of land plants. *Fieldiana Botany* 47: 17-33.

Niklas, K. J. 2014. The evolutionary-developmental origins of multicellularity. *American Journal of Botany* 101: 6–25.

Oltmanns, F. 1898. Die Entwickelung der Sexualorgane bei *Coleochaete pulvinata*. *Flora* 85: 1-14.

Pringsheim, N. 1860. Beiträge zur Morphologie und Systematik der Algen. III. Die Coleochaeteen. *Jahrbücher für wissenschaftliche Botanik* 2: 1-38.

Ruhfel, B. R., M. A. Gitzendanner, P. S. Soltis, D. E. Soltis, and J. G. Burleigh. 2014. From algae to angiosperms—inferring the phylogeny of green plants (Viridiplantae) from 360 plastid genomes. *BMC Evolutionary Biology* 14: 23.

Searles, R. B. 1980. The strategy of the red algal life history. *American Naturalist* 115: 113–120.

Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108: 499-506.

Svedelius, N. 1927. Alternation of generations in relation to reduction division. *Botanical Gazette* 83: 362-384.

Wesley, O. C. 1930. Spermatogenesis in *Coleochaete scutata*. *Botanical Gazette* 89: 180-191.

Wettstein, F. v. 1943. Warum hat der diploide Zustande bei den Organismen den größeren Selektionswert? *Naturwissenschaften* 31: 574–577.

Figure 1: Maternal resources are optimally allocated when each zoospore receives $\hat{x}$ which is less than x^*, the investment per zoospore at which $f(x^*) = 2f(x^*/2)$. Therefore, $\hat{x}$ is better left undivided because allocation of $\hat{x}$ to two zoospores each receiving $\hat{x}/2$ yields a lower return on investment than allocation of $\hat{x}$ to a single zoospore.

Figure 2: A zygospore divides to produce m zoospores. Provisioning costs per zoospore, x, are represented to the right of the origin and accessory costs per zoospore, a, to the left. The optimal value of x increases with a where a^* is the accessory cost per zygospore at which $f(x^*) = 2f(x^*/2)$. At this critical size, equal fitness is obtained by dividing mx^* among m or $2m$ zoospores (leftward arrow). Accessory costs per zoospore are halved for $2m$ zoospores with the new optimal level of provisioning $\tilde{x}$.